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The Role of Fire and Soil Resources in Forest-Savanna Structure and Transition Dynamics

O Papel do Fogo e de Recursos do Solo na Estrutura e nas Dinâmicas de Transição de Floresta-Savana

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Os membros da Comissão Examinadora acima assinaram a Ata de defesa, que se encontra no processo de vida acadêmica do aluno.

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ao meu irmão Pedro, à toda minha família
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Mas que sabe ler o seu mundo.
Nesse universo de outros saberes, sou eu o analfabeto.”
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RESUMO

Tem sido sugerido que florestas e savanas são estados alternativos da vegetação sob certos regimes de chuva e condições do solo. Uma série de *feedbacks* são responsáveis pela manutenção de cada estado, incluindo um *feedback* vegetação-fogo, que é de notável importância na manutenção das savanas em regiões tropicais úmidas ao redor do mundo. Em florestas, onde o subosque é pouco iluminado, o crescimento de gramíneas C4 intolerantes à sombra é inibido, e um microclima úmido é criado simultaneamente, impedindo a ocorrência de incêndios frequentes e intensos, permitindo a persistência de espécies susceptíveis ao fogo. Em savanas, a alta disponibilidade de luz no sistema permite o acúmulo de biomassa de gramíneas C4, o principal combustível do fogo, favorecendo incêndios frequentes e intensos que impedem o fechamento do dossel e promovem a persistência de espécies tolerantes ao fogo. Além do fogo, propriedades do solo e alguns distúrbios frequentemente afetam florestas e savanas, e suas dinâmicas de transição. Por exemplo, a disponibilidade de recursos no solo pode exercer um efeito na taxa de crescimento de árvores. Tal efeito afeta o tempo requerido para que a comunidade se feche o suficiente para resultar na supressão de espécies intolerantes à sombra e inibição do fogo. Este trabalho objetivou avaliar como fatores que influenciam transições floresta-savana (i.e. atividade do fogo, disponibilidade de recursos e suas interações) afetam sua dinâmica. Para avaliar tais influências, variações nas características funcionais de comunidades distribuídas ao longo de um gradiente floresta-savana foram analisadas e comparadas entre paisagens com diferentes regimes de fogo e recursos no solo. Encontramos fortes evidências de que distinções na atividade do fogo estão induzindo diferenças na estrutura de savanas, e que recursos do solo podem ter um papel indireto, através da modulação do fogo pela regulação na produtividade de gramíneas C4. Nossos resultados também indicam que diferenças na atividade do fogo podem provocar distinções na relação entre adensamento da comunidade e limiares funcionais entre florestas e savanas. Na paisagem que queimou mais frequentemente, o limiar funcional ocorreu em comunidades mais abertas. A magnitude da mudança em parâmetros funcionais também foi maior na área que apresentou atividade do fogo mais frequente e diferenças mais marcantes nos recursos do solo em cada estado da vegetação. A paisagem com períodos maiores sem incêndios e pouca diferença nos recursos do

solo entre florestas e savanas apresentou menores magnitudes, sugerindo que a atividade do fogo e propriedades do solo estão agindo em conjunto para suavizar a transição. Nosso estudo evidenciou a importância do fogo e de recursos do solo para transições floresta-savana na escala de paisagem. O fogo age de maneira intensa e direta, resultando em savanas mais abertas e maior distinção nos atributos funcionais entre savanas e florestas onde sua ocorrência é mais frequente. Maiores diferenças na disponibilidade de recursos do solo entre savanas e florestas de uma paisagem resultam em diferenças mais acentuadas nos atributos funcionais das comunidades em cada estado. Sozinhos, eles podem afetar a dinâmica de comunidades, e suas interações podem acentuar ou amenizar a dinâmica da transição.

ABSTRACT

Forests and savannas have been suggested to be alternative vegetation states under certain precipitation regimes and soil conditions. A series of feedbacks are responsible for maintaining each state, including a fire-vegetation feedback, which is of remarkable importance to maintain the savanna state in wet tropical regions worldwide. In closed canopy forests, the very shaded understory inhibits the growth of shade-intolerant C4 grasses while creating a moist microclimate, which prevents the occurrence of frequent and intense fires, permitting the persistence of fire-susceptible species. In open canopy savannas, the high light availability in the system promotes high levels of C4 grass biomass, which is fuel for fire, favoring the occurrence of frequent and intense fires, which prevent canopy closure and promote the persistence of fire-tolerant species. Besides fire, soil properties and some disturbances frequently affect forests and savannas, and their transition dynamics as well. Soil resource availability, for instance, can exert an effect on tree growth rate. This effect affects the time required for the community to reach a closure level that will result in the suppression of shade-intolerant species and fire inhibition. This work aimed to evaluate how the factors influencing forest-savanna transitions (i.e. fire activity, resources availability and their interactions) affect their dynamics. To evaluate such influences, we analyzed variations of the vegetation functional traits at the plant communities distributed along a forest-savanna gradient, and compared them between landscapes with distinct fire regimes and soil resource availability. We found strong evidence that distinct fire activity is inducing differences in savanna structure, and that soil resources may have an indirect role, by modulating fire through C4 grass productivity. Our results also indicated that different fire activity may be provoking distinction in the relationship of community densification and functional thresholds between savannas and forests. At the landscape that burned more often, the functional threshold occurred at more open communities. The magnitude of the functional traits change between forests and savannas was also larger in sites with more frequent fire activity and more marked differences in soil resources of each vegetation state. The landscape with longer fire-free intervals and little difference in soil resources between forests and savannas presented shorter magnitudes, suggesting that both fire activity and soil properties are acting together to smoothen the transition. Our study evidenced the importance of both fire and soil

to forest-savanna transitions at the landscape scale. Fire acts directly and strongly, resulting in more open savannas and higher differences in the functional traits between forests and savannas, where it occurs more frequently. More marked differences in soil resource availability between forests and savannas within a landscape result in more accentuated differences in the functional traits of the communities at each state. Each one alone may affect community structure and dynamics, and their interactions may accentuate or mitigate the transition dynamic.

SUMMARY

1. INTRODUCTION

In a global scale, precipitation regulates biome distribution through direct influence over primary productivity (Rosenzweig 1968; Lieth 1973; Polis 1999). Regions with high levels of precipitation facilitate tree development, allowing them to occupy most of the open spaces and outcompete the herbaceous layer, and form closed canopies characteristic of forest communities (Walter 1971; Scholes & Archer 1997). On the dry extreme, low mean annual precipitation (MAP) limits woody cover, preventing canopy closure and sometimes permitting tree-grass coexistence, resulting in savannas, grasslands and deserts (Scholes & Archer 1997; Sankaran *et al.* 2005). Seasonality also displays a fundamental role, as the length of the dry season may influence savanna distribution worldwide (Good & Caylor 2011; Lehmann *et al.* 2011). Wherever the MAP displays intermediate levels and seasonality is present, however, both savanna and forest landscapes are observable, suggesting that factors other than climate are driving tropical biome distribution (Staver *et al.* 2011a, 2011b).

In some tropical regions where precipitation and soil nutrients are not limiting tree establishment, and a precipitation seasonality pattern that allows fire occurrence is present, there is a co-occurrence of forests and savannas (Hirota *et al.* 2011; Staver *et al.* 2011a, 2011b; Hoffmann *et al.* 2012). Soil resources (i.e. nutrients and water availability) exert strong influence in vegetation distribution, particularly at local scales, and fire presence is also pointed as an important factor maintaining savannas where forests could happen (Bond *et al.* 2005; Hoffmann *et al.* 2012). The MAP range at which both forests and savannas can occur is not consensual among authors, ranging from 650 to 2500 mm in the least conservative estimates (Sankaran *et al.* 2005; Staver *et al.* 2011a, 2011b).

Ecosystems are rarely static. Instead, they are always subjected to changes in conditions (e.g. precipitation level, soil nutrients) and to external disturbances (e.g. extremely intense fires, extreme droughts). These can result in gradual changes in the system state (e.g. decrease in tree cover), population fluctuation and other modifications in the system dynamics. Whilst the effects on ecosystem dynamics created by internal or external drivers are difficult to disassemble, temporal variance is present, and a dynamical complex system is

rather more realistic than a stable one (Scheffer & Carpenter 2003). Thus, it would be better to substitute words such as “stable states” and “equilibrium” by “attractors”, for instance, when working with complex dynamic systems (Scheffer & Carpenter 2003). The multi-stability theory is a good way of explaining forest-savanna co-occurrence and transition dynamics in the tropics (Scheffer *et al.* 2009; Warman & Moles 2009). Following this theory, forests and savannas are alternative vegetation states (or attractors), which are maintained by a series of environmental conditions and feedbacks. If the conditions of the system changes extremely (e.g. precipitation level, soil nutrients), or if it is perturbed by an external and strong enough disturbance (e.g. extreme drought event, deforestation), the system may shift abruptly to another state, and then will start to be maintained by a series of different feedbacks. Regarding the forest-savanna case, soil resources and precipitation may influence the community structure dynamic (e.g. time to reach a sufficient canopy closure that inhibits fire), thus influencing fire-vegetation feedbacks, which in turn are constantly affecting the system equilibrium (Bond *et al.* 2005; Hoffmann *et al.* 2011, 2012). Some parameters, however, should be treated differently according to the system in question. Fire occurrence, for instance, is common in savanna ecosystems, and thus should be treated as a condition, which in turn is susceptible to variations (e.g. regarding frequency and intensity). In forests, however, fire is stochastic and frequently destructive, and thus should be treated as a disturbance (Bond *et al.* 2005; Ratnam *et al.* 2011).

In savanna landscapes, the continuous C4 grass layer works as fuel to fires, commonly after the dry season. Fire top-kills fire-sensitive tree saplings, promoting communities with sparsely distributed woody plants (hereafter open communities; Bond *et al.* 2005; Bond 2008; Hoffmann *et al.* 2012). Individuals that are well adapted to fire occurrence will survive after fire and resprout (Hoffmann *et al.* 2003, 2012). The resulting conditions, with high light availability, are favorable for shade-intolerant C4 grasses, which form a continuous layer as soon as soil water availability reaches propitious levels. This vegetation-fire feedback allows savanna occurrence in regions where precipitation and soil resources are high enough to allow the development of forest communities (Bond *et al.* 2005; Staver *et al.* 2011a, 2011b; Hoffmann *et al.* 2012). In contrast, forest communities are characterized by closed canopies and shaded understory, excluding C4 grasses and, therefore,

inhibiting fire occurrence. The resulting extremely low fire frequency allows the establishment and growth of shade-tolerant and fire-susceptible tree species, reinforcing canopy closure and the forest system resistance (Hoffmann *et al.* 2003, 2012; Bond *et al.* 2005; Staver *et al.* 2011b).

Several natural and anthropogenic factors can modulate fire frequency and intensity. In protected areas, fire suppression due to management practices may result in longer fire free periods. Humans can also trigger fires (on purpose or not, when clearing areas with vegetation or when activities involving fire run out of control, respectively), increasing fire frequency in some areas. Among the natural factors, precipitation regime and soil resources are of significant importance. Sites with low productivity due to low soil resources and/or low precipitation may limit fire spread through low fuel availability and continuity, while high productivity in places with higher rainfall is often associated with very high fuel moisture, inhibiting fire ignition and spread (Dantas & Pausas 2013; Pausas & Ribeiro 2013). Thus, fire activity in a global scale displays a humped relationship with productivity (Pausas & Ribeiro 2013). At landscape scale, nutrient availability can also affect grass productivity, an important component of flammability, modulating the climate-fire relationship (Scholes 1990). In landscapes where productivity is high enough to create a continuous grass layer and a dry season is present, fire activity tends to be much more frequent and intense. In these landscapes, soil resources differences may result in fire regime differences (i.e. soils with more resources would increase the grass layer biomass and continuity, increasing fire frequency and intensity). Thus, in regions with higher fire frequency, fire should prevent the formation of a dense woodland savanna, and the transition from savanna to forest should be sharper and also limited by the occurrence of long fire-free periods or of patches with high soil nutrient availability (Rossatto *et al.* 2009; Hoffmann *et al.* 2012; Pausas & Ribeiro 2013).

Besides the indirect effect of nutrient availability on fire activity, soil resources exert a direct effect over the savanna-forest transition dynamics. Soil resource availability affects tree growth, and the likelihood of a transition from a savanna to a forest depends directly on this influence (Hoffmann *et al.* 2012; Murphy & Bowman 2012). As tree growth rates depends on soil resource availability, the probability of forest species invading a savanna community changes accordingly

(Hoffmann *et al.* 2012). Thus, the contrasting growth patterns of forest and savanna tree species may result in distinct structural features of forest-savanna transitions under soil with high and low resources (Falster & Westoby 2003; Hoffmann *et al.* 2003; Lawes *et al.* 2011).

The differences comprising forests and savanna are not only structural. Each state presents distinct functionality, as well, resulting from the contrasting functional traits of its species. Plant functional traits are easily measured characteristics that gives us insights on the individual performance and ecological role (Violle *et al.* 2007; Ratnam *et al.* 2011). Ratnam *et al.* (2011) suggested a set of morphological, physiological and life-history traits which can be used to distinguish forest and savanna communities. Some of these characteristic traits include greater stem height and higher specific leaf area in forest species, which suggests fast growth plant strategy. In other words, forest trees are able to establish and grow hastily if sufficient resources are available and can survive in the shaded understory of forest communities (Westoby 1998; Falster & Westoby 2003). Savanna individuals, in contrast, often present higher investments in bark thickness instead of stem height (Ratnam *et al.* 2011). Thus, using individual functional information averaged to the community level (i.e. functional parameters; Violle *et al.* 2007) is a powerful way to study vegetation states transition and processes changes at the landscape scale (Ratnam *et al.* 2011; Dantas *et al.* 2013).

The coexistence of plants under a set of conditions is explained by a complex variety of traits, related to the ability that a plant posses of dealing with environmental variations and disturbances. This set of traits may reflect trade-offs between resistance and recovery to particular disturbances (Miller & Chesson 2009; Enright *et al.* 2014). While the investment of resistant species is concentrated in minimizing the effect of disturbances through persistence, resilient species tend to invest more in traits that help to recover from disturbances (Miller & Chesson 2009). Modeling the distribution of community functionality through functional traits along vegetation gradients, and relating these traits with resistance/resilience could help in the detection of critical points (thresholds) at which vegetation abruptly shifts to an alternate state, as well as in the understanding of mechanisms underlying the transition dynamics (Dantas *et al.* 2013). As savannas and forests are subjected to distinct environmental conditions and levels of disturbances at a local scale, it is

expected that the plants at each state present a very different set of traits. While trees that invest more in bark thickness than in other traits present an advantage in savanna landscapes, trees that are able to grow in height hastily present a better chance to survive in forest landscapes, for instance (Falster & Westoby 2003; Lawes *et al.* 2011; Ratnam *et al.* 2011). Thus, it is expected that a functional threshold occurs between savanna and forest communities, as the plant functional traits in them differ drastically (Ratnam *et al.* 2011; Dantas *et al.* 2013). As environmental conditions and disturbances affect directly the occurrence of plants with distinct functional traits and the presence of a threshold between states, differences in them should interfere in the characteristics of the community at which this threshold occurs. Understanding better this relationship is one of the objectives of our study.

Studying the dynamics of forest-savanna transitions and how soil resources and fire activity interfere in these dynamics is of substantial importance for a better understanding of the ecology of these systems, and for their conservation in the tropics. The Cerrado (Brazilian savanna) is the second most extensive biome in South America. Springs of three of the most important watersheds of the continent are located inside the Cerrado domain, along with a global biodiversity hotspot recognized as the richest savanna of the world (Ratter *et al.* 1997; Myers *et al.* 2000; Silva & Bates 2002). The role of fire maintaining the Cerrado biome must be evidenced, and fire control policies must consider fire not only as a threat, but also as an ally, as the dynamics of Cerrado communities continually occur alongside wildfires through millions of years. Fire exclusion would lead to potential forest invasion in some regions, implying in loss of Cerrado biodiversity (Bond *et al.* 2005). In the context of a changing world climate, alterations in precipitation regimes (which directly affect fire activity) could lead to changes in the distribution of these two systems (Beier *et al.* 2012; IPCC 2014). Thus, understanding how distinct fire regimes interfere in the transition dynamics is critical.

Our objective in this study was to better understand how fire and soil resources influence forest-savanna transitions. Therefore, we investigated plant functional traits and soil features thresholds, in savanna-forest structural gradients, in two landscapes with contrasting fire regimes. Specifically, we focused on evaluating the role of fire and soil resources, directly and/or indirectly, on the processes shaping forests and savannas and their transition dynamics. Thus, we assessed information

of community functionality in forests and savannas, in regions with contrasting soil resource availability and fire regimes, in order to correctly interpret the mechanisms influencing the spatial transition of these two systems and to answer the following questions:

(1) How soil properties and fire activity affect the structure of savannas and forests at local scale?

(2) How the location and magnitude of functional trait thresholds in savanna-forest gradients differ between sites with distinct fire regimes and soil resource availability?

We hypothesized that (1) soil resources and fire activity directly influence forest-savanna structures and transitions, favoring distinct growth strategies according to resources availability, and promoting the persistence of individuals with distinct traits under different fire regimes. As high soil nutrient concentrations positively affect tree growth rates and favors species with a fast-growth strategy, we expected to find taller communities with thinner bark (lower bark development allows investment in other traits) and higher SLA, which are characteristic of fast-growing species (Poorter & Remkes 1990; Reich *et al.* 1992; Westoby 1998; King *et al.* 2006). Fire, in turn, may exclude individuals with this kind of growth strategy, as they are not able to survive and resprout. Frequent fire may then favor the occurrence of tree species that invest more in bark thickness than in other traits (e.g. height, SLA, wood density), in order to grant protection from fires (Falster & Westoby 2003; Hoffmann *et al.* 2003; Lawes *et al.* 2011, 2013). Thus, we expected to find savannas and forests to be denser (higher community closure) and taller where resources availability is higher and fire intervals are longer, what would support our first hypothesis. However, in landscapes where fire activity is frequent and soil resource availability is high as well, we expected that fire negative influence would surpass soil resources positive influence on tree height and community closure, as longer time periods are needed to observe the latter.

We also hypothesized that (2) regions that burn more frequently and present higher differences of soil resources between savannas and forests tend to present more accentuated transitions. Frequent fire activity will result in a stronger selective pressure exerted by fire. In places where fire occurs frequently, the

importance of having fire-protection traits well developed rises. This may result in more marked traits differences when comparing forest and savanna communities. Higher fire frequency may also interfere at the level of community closure at which the functional threshold happens, as landscapes with frequent fire will not allow further closure of savanna communities (Falster & Westoby 2003; Hoffmann *et al.* 2003; Bond *et al.* 2005; Lawes *et al.* 2011, 2013; Staver *et al.* 2011a). Higher differences in soil resources between forest and savanna at a landscape may also interfere in traits distinctions between these two vegetation states. As high soil nutrient availability affects growth rates positively and shorten the fire-free period necessary for a community to become denser, landscapes where soil resources distinction is more marked between forests and savannas may present more marked community traits differences, as well (Reich *et al.* 1992; Westoby 1998; Hoffmann *et al.* 2012). We expected to find functional thresholds in more open communities, and a larger magnitude of trait changes at sites with more frequent fire activity and more marked differences in soil resources. These results would help to support our second hypothesis.

2. MATERIAL AND METHODS

2.1 Study Sites

The present study was carried out at the ecological reserve of the "Instituto Brasileiro de Geografia e Estatística" (IBGE) (15°55'8" - 15°57'53"S and 47°51'26" - 47°54'10"W) and at a preserved area of the Financial Administration School (ESAF) (15°51'38" - 15°52'22"S and 47°49'15" - 47°49'45"W), both located inside the environmental protection area "Gama-Cabeça de Veado" and being part of the same landscape (Fig. 1). This study site is located inside Distrito Federal, a Brazilian federative unit in the Midwest region, part of the Brazilian Central Plateau (Fig. 1A). According to Köppen (1931) classification, the climate is tropical humid (Aw), with a dry season from May to September, and a wet season from October to April. The mean annual precipitation of the region is around 1700 mm (Cardoso *et al.* 2014). The mean monthly temperature of the warmest month (October) is 25.3 °C, while the temperature of the two coldest months (June and July) is 20.8 °C, being the mean annual temperature around 22 ºC (Pereira *et al.* n.d.; Cardoso *et al.* 2014). The

altitudes range from 1048 to 1150 meters, and the soil is characterized as a yellowish-red Oxisol with clay texture (IBGE 2004; Quesada *et al.* 2004).

We also used data from Dantas *et al.* (2013) collected at Emas National Park (ENP), during the wet season from 2009 to 2011. ENP is located in the southwest of the state of Goiás (17°49' - 18°28'S and 52°39' - 53°10'W), and as the IBGE Reserve, is part of the Brazilian Central Plateau (Fig. 1A). Following Köppen (1931) classification, the climate is tropical humid (Aw) with two well defined seasons with intervals matching the ones of the IBGE Reserve and ESAF plot set. The mean annual precipitation of the region is around 1745 mm, and the mean temperature lies around 24.6 °C (Cianciaruso *et al.* 2005). The altitudes range from 720 to 888 meters, and the prevalent soil type is a dystrophic Oxisol (Ramos-Neto & Pivello 2000; Dantas *et al.* 2013).

Inside the IBGE Reserve and ENP, the predominant vegetation is the Cerrado, which is composed by a mosaic of different vegetation types, varying from dense woody physiognomies with a closed or semi-closed canopy and low grass occurrence (forest-like structure), to physiognomies with sparse and less frequent woody plants and a continuous grass cover (savanna-like structure) (Oliveira-Filho & Ratter 2002; IBGE 2004; Dantas *et al.* 2013). The ESAF area is mainly composed of forest, with dominant tall woody vegetation, low grass cover and closed canopy. Fire suppression policies are being applied since the year of establishment of the IBGE Reserve (1978), although some fires, triggered by natural and anthropogenic sources, still occur. No fires were reported inside ESAF for more than 30 years. On the other hand, natural fires are allowed inside ENP since 1994, with a spread control policy done by annually burned firebreaks (Ramos-Neto and Pivello 2000; personal contact). Therefore, the landscapes are submitted to distinct fire regimes for 22 years. The IBGE Reserve and ESAF plot set will be referred as "IBGE" from this point on.

2.2 Field Campaign

In each of the two landscapes we distributed plots comprising a forest-savanna vegetation structure gradient (Figs. 1B, 1C, 1D). At ENP 100 plots of 5 x 5 m were allocated whereas at IBGE 50 plots of 10 x 5 m were sampled. To ensure that a vegetation structure gradient was sampled, plots were distributed using a

stratified design based on classes of either time since last fire (ENP) or tree cover (IBGE). For this purpose, the tree cover classes used at IBGE were 100 - 60%, 59 - 40%, 39 - 20% and 19 to 0%. Although the design was planned to include an equal number of plots within each class, for practical reasons, two savanna plots had to be discarded at ENP and only 98 plots were used. In addition, since all the plots which were unburned for more than 15 years ended up being small and dense forest fragments with difficult access, the 20 forest plots had to be distributed systematically along a trail (see Dantas *et al.* 2013 for more details). Finally, as we used four tree cover classes at the IBGE sampling and 50 plots, the lowest percent tree cover class included 14 plots while other classes included 12.

The sampling took place during the wet season of 2014 - 2015 for IBGE and of 2009 - 2010 and 2010 - 2011 for ENP. In both cases it was possible to collect data from the whole forest-savanna structural gradient. Plots that were assigned to inaccessible areas (legal and natural issues) were replaced by other random plots respecting the sampling design. We also substituted plots that contained less than three woody individuals (perimeter at ground level < 10 cm) and less than two species.

In each plot, we labeled and numbered every individual with at least 10 cm of ground-level perimeter. We measured functional traits of these individuals in the field (i.e. tree height, stem bark thickness and stem perimeter at ground level) as well as collected leaf and branch samples to measure other traits (i.e. specific leaf area and wood density; see item 2.3). We also collected soil samples (0 to 10 cm) in order to acquire physical and chemical characteristics for the soils at each plot. All of these attributes and parameters have let us test for the presence of breakpoints inside the forest-savanna gradients, which indicate critical transitions from one vegetation state to another (Dantas *et al.* 2013).

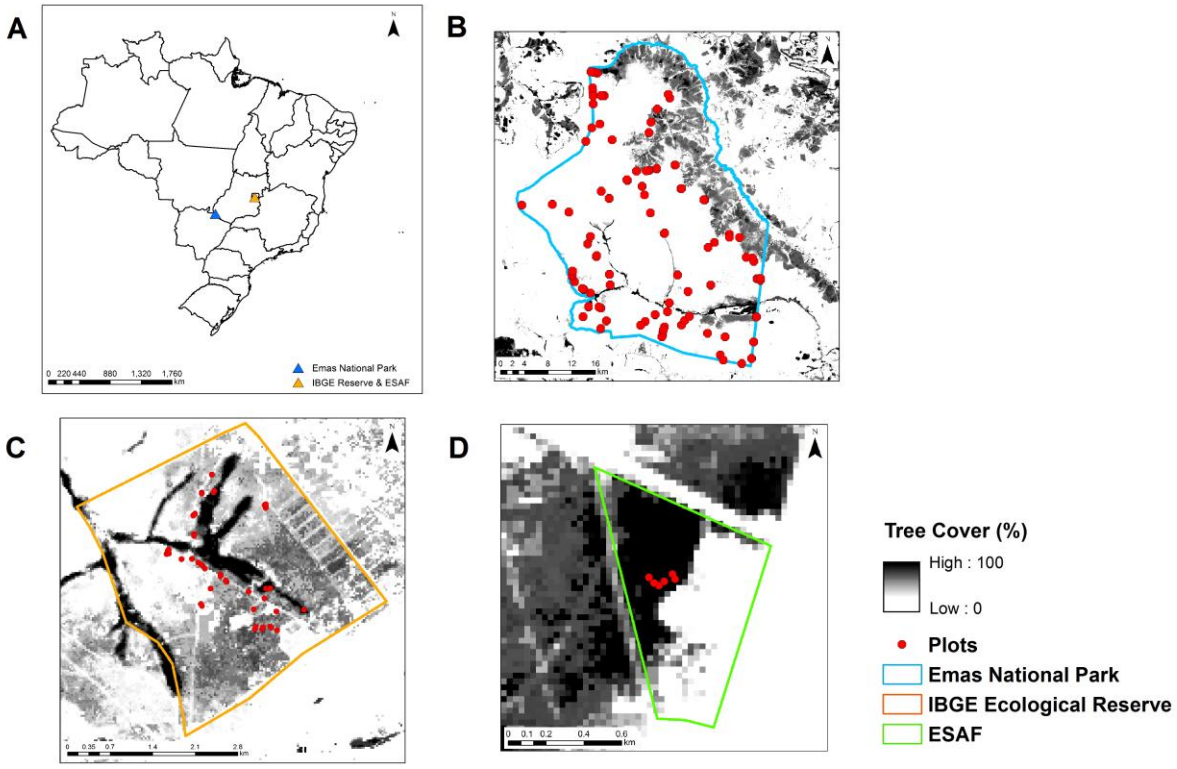

Figure 1: Location of the study sites inside Brazil and tree cover maps of the protected areas. The areas inside Distrito Federal, which are the IBGE Reserve and ESAF, are approximately 10 kilometers apart (A). Protected area borders are represented by different colors, as stated by the figure legend (B, C, D). Tree cover maps obtained from Hansen *et al.* (2013).

2.3 Laboratory Analysis

We collected five leaf samples per individual to determine specific leaf area. Following Pérez-Harguindeguy *et al.* (2013) the leaves were labeled and scanned, while still fresh, in order to obtain their area using the ImageJ software (US National Institutes of Health). The leaves were then oven dried at 70 °C for at least 72 h, or until a constant weight was obtained (Pérez-Harguindeguy *et al.* 2013). Specific leaf area (SLA) was then calculated dividing the fresh area by the dry mass for each replicate, and then averaged, resulting in a single SLA per individual.

To estimate wood density, we measured the diameter and the length of the collected branches while still fresh with a caliper. Two perpendicular diameter measurements were taken after removing the branches bark in the same location. We estimated branch volume considering that the branches were cylinder-shaped. After obtained the branch volume, the samples were oven dried at 70°C for at least 72h, or until a constant weight was obtained (Pérez-Harguindeguy *et al.* 2013). Wood density for each individual was calculated dividing the sample mass by its volume.

Relative stem height and relative bark thickness were calculated by dividing stem absolute height and bark thickness by stem diameter, in order to get a view of plant strategies that is independent from ontogeny, reflecting inherent differences between species (Lawes *et al.* 2013). Therefore, the final analysis included four functional traits: relative height, relative stem bark thickness, SLA and wood density. Using functional traits was important to our analysis as they are relatively easy to measure attributes that reflect both ecological strategies and evolutionary history, give us insights of how plants and communities respond to environmental conditions, and how they influence ecosystem properties (Ratnam *et al.* 2011; Pérez-Harguindeguy *et al.* 2013). Thus, we could use them to test for changes in the functionality of the system in the forest-savanna boundary.

The soil samples were oven dried like the leaves and branches, and then sent to the Soil Science Department of University of São Paulo (ESALQ/USP) for physical and chemical analysis (e.g. nitrogen, phosphorus, potassium, calcium, aluminum, magnesium, organic matter, sand, silt and clay concentration, and cation exchange capacity).

2.4 Fire Activity

In order to access IBGE fire history, we downloaded a Landsat time-series from 1985 to 2014 through the USGS Global Visualization Viewer website. Loading these images in ArcGIS 10.1 (ESRI Inc.) software and adding the coordinates of our plots made it possible to check for fire scars in each image and then get information about the exact month in which each plot burned. We then calculate fire frequency, time since last burn and mean fire interval (calculated as the inverse of fire frequency) for each plot. We assigned a 30-year fire interval (maximum obtained) for plots that did not burn during the observed period. For ENP, the methodology was similar, but the time series ranged from 1979 to 2010, and the maximum fire interval assigned for plots that did not burn during this period was of 32 years. Through fire history, we could test for significant differences in the fire regimes of the landscapes.

2.5 Data Analysis

To quantify the degree of closure in vegetation structure of each plot, we used the metric suggested by Dantas *et al.* (2013): the Community Closure Index

(CCI), as named by the authors. The CCI is calculated as the logarithm of the total volume occupied by all woody individuals inside the plot, that is, the sum of the volume occupied by individual trees, assuming that each tree has a cone shape. It was standardized to vary from zero (more open community) to one (more closed community). The CCI made it possible to check at which level of community closure the functional thresholds occurred at each landscape.

To test for differences between the fire regimes of IBGE and ENP, we used a Wilcoxon test to compare the mean fire interval and time since last burn between sites. We looked for structural modifications in the functional traits over the CCI gradient using the "strucchange" package of R Environment (Zeileis *et al.* 2002, 2003; R Development Core Team 2015) to test for breakpoints in the data. When a breakpoint was found for a functional trait, we then fitted a linear regression, and a piecewise regression applying the breakpoint value found for the trait-CCI relation. The objective of fitting a piecewise regression is that it is a statistical way of identifying ecological thresholds (Toms & Lesperance 2003). To check which model fitted better, we compared the corrected Akaike information criterion (AICc) for each model. When a significant breakpoint occurred and the piecewise model fitted the data better than a linear model, showing lower AICc values, we interpreted as evidence of a true threshold relationship between the CCI and the parameter being tested. Finding a threshold relationship indicated an abrupt change in the functionality of the system, and checking at which CCI these thresholds occurred at each landscape made it possible to test for differences in soil resources and fire activity affecting the level of community closure at which the change occurred. We log-transformed the data when necessary to improve normality of the residuals. Finally, we calculated the confidence interval of the breakpoints to test whether their location significantly differed between the two landscapes. When the confidence intervals did not overlap, a significant difference was assumed. The same analysis methods were applied to test for breakpoints in soil traits.

We also calculated the magnitudes of change for the breakpoints that presented a threshold relationship within the CCI gradient using the method suggested by Verbesselt *et al.* (2010). The magnitude was calculated as the difference between the parameter value for each segment at the CCI breakpoint in the fitted piecewise regression model. With the absolute values of magnitudes, we

tested for differences between landscapes using a Student's t-Test, and then checked if fire and/or soil resource availability were influencing the magnitude of change of the traits.

At each site, the mean breakpoint of all parameters (plant functional traits and soil properties) that presented a significant threshold relationship along the CCI gradient was used to separate forest plots from savanna plots. This separation made it possible to compare soil resource availability, plant functional traits and fire activity between vegetation states and landscapes. The comparison was made with an ANOVA followed by a Tukey's honest significant difference test. Finally, we fitted a multiple regression in order to check which parameters were more strongly influencing the vegetation community structure at each site. All analyses were performed in R Environment (R Development Core Team 2015) with the packages "vegan", "nlme", "strucchange", "segmented" and "AICcmodavg" (Zeileis *et al.* 2002, 2003; Muggeo 2003, 2008; Oksanen *et al.* 2015; Mazerolle 2016; Pinheiros *et al.* 2016).

3 RESULTS

The sampling at IBGE consisted of 548 individuals of 114 species, and at ENP 554 individuals of 88 species.

3.1 Fire Activity

As almost none of the forest plots at IBGE burned during the years of the analyzed time series (except two of them which burned once), the mean fire interval for these plots was 30 years. Due to a huge fire that occurred at the IBGE Reserve in 2011, which burned almost the whole Reserve, including almost all the savanna area where we posteriorly set up plots to sample in 2015, the time since last burn was really short for the majority of IBGE plots (Fig. 2B). None of the forest plots at ENP burned during the examined period, but in general, considering both forest and savanna plots, the plots there burned more frequently when compared to IBGE plots (Fig. 2).

The Wilcoxon test showed the fire activity distinction between both studied areas (Fig. 2), as expected, making it possible for us to test the influence of distinct fire regimes to the transition dynamics. Even though the two areas are inside the same climate envelope, some other factor is modulating differently the fire regimes. Therefore, hereafter, we refer to these areas as High (HFL) and Low (LFL) Fire Landscapes, respectively for ENP and IBGE.

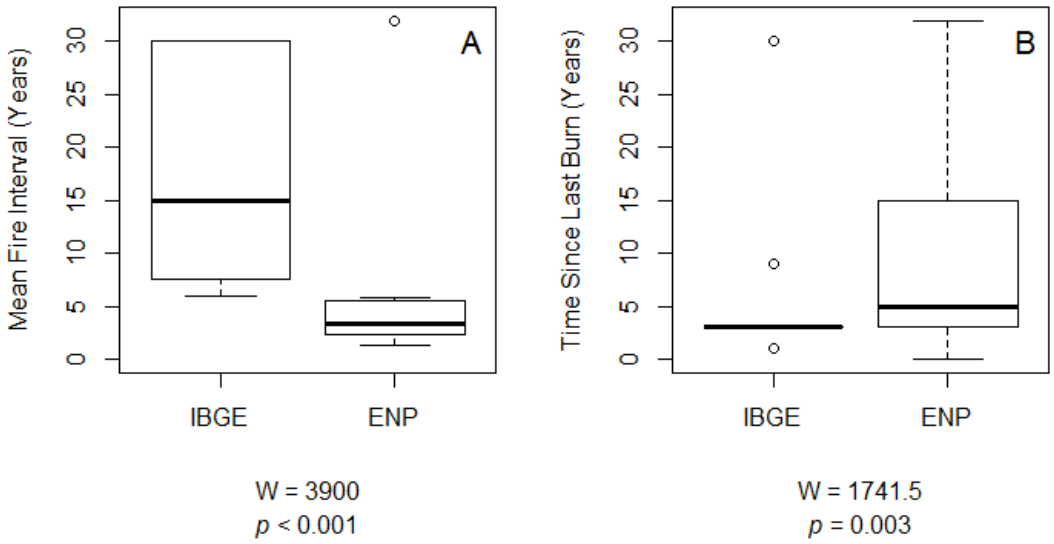

Figure 2: Fire activity comparison between IBGE (Low Fire Landscape) and ENP (High Fire Landscape). The shorter mean fire interval (A) presented at ENP indicates a more frequent fire action when compared to IBGE. The low values of time since last burn at IBGE (B) are explained by a huge fire that burned almost the whole reserve in a recent year. Values of *p* and of the Wilcoxon test (W) presented in the figure.

3.2 Functional Trait Breakpoints

In general, we noticed that trees with high investment in height growth for a certain diameter (high relative height) are more common in more closed communities, while the opposite happens in more open communities (Figs. 3A, 3B). Trees in more open community plots (composed mostly by savannas) invest in other attributes instead, e.g. higher relative stem bark thickness (Figs. 3C, 3D). Higher values of specific leaf area (SLA) and wood density were also observed in more closed communities when compared to more open ones (Figs. 3E, 3F, 3G, 3H).

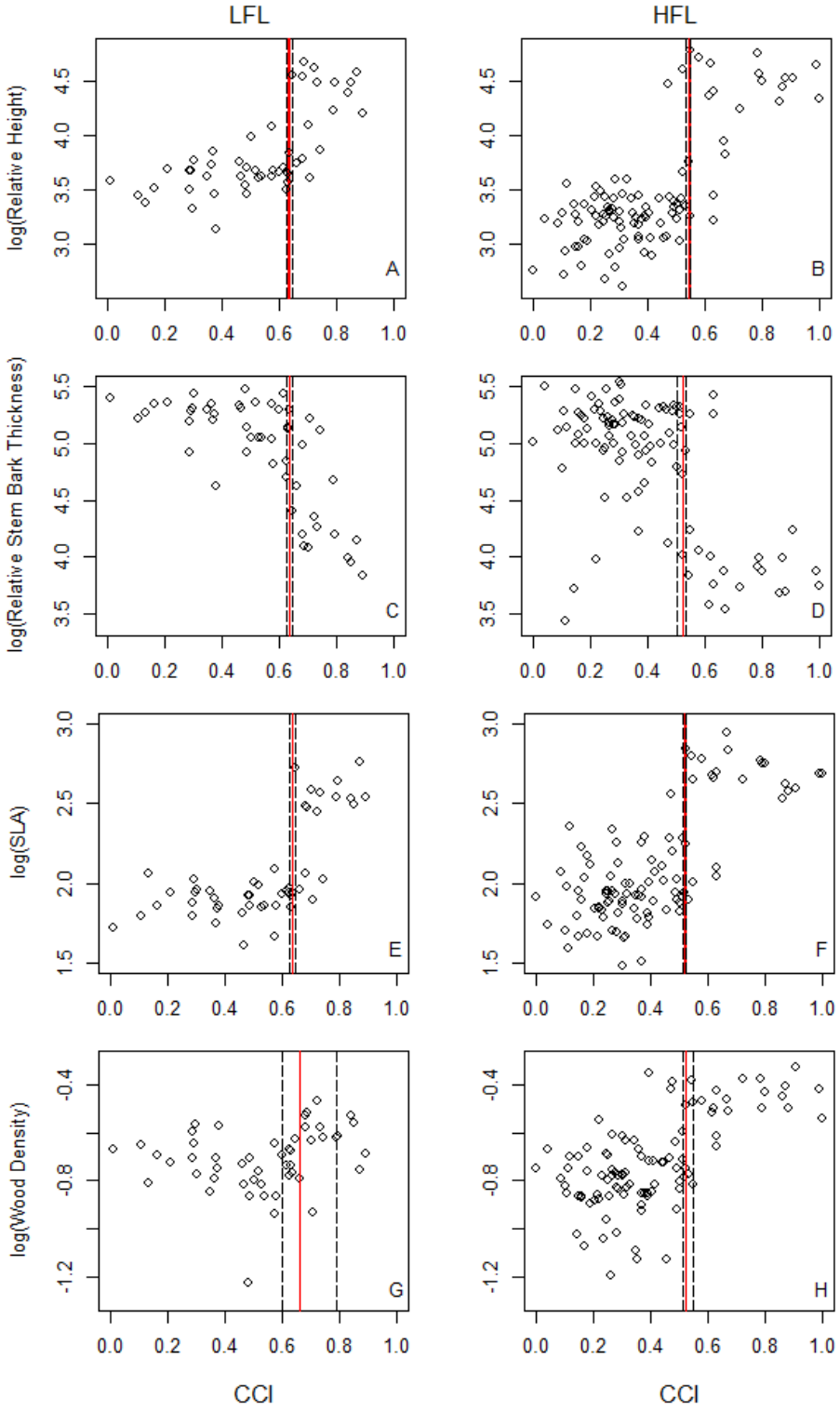

Figure 3: Functional traits thresholds in a Community Closure Index (CCI) gradient at the Low (LFL) and High (HFL) Fire Landscape. The parameters presented are relative height, relative stem bark thickness, specific leaf area and wood density for the LFL (A, C, E and G, respectively) and the HFL (B, D, F and H, respectively). The breakpoints are represented by solid red lines, and the confidence intervals by dashed black lines. It is observable how the threshold occurs in more closed communities at the LFL when compared to the HFL. All breakpoints were significant ($p < 0.05$).

For the relative height, relative stem bark thickness, SLA and wood density attributes the breakpoint was significant in both sites (Fig. 3; Table 1), and occurred in more closed communities at the LFL when compared to the HFL. In all cases, the piecewise model fitted better than the linear one (Table 2), indicating the existence of a functional threshold in the community closure gradient for all those parameters. The confidence interval for each trait breakpoint at the LFL did not overlap the ones at the HFL (Fig. 3; Table 1), showing evidence that the thresholds in fact occur at distinct levels of community closure when comparing both landscapes.

Table 1: Functional traits breakpoints in a Community Closure Index (CCI) gradient at the Low (LFL) and High (HFL) Fire Landscape. When the confidence intervals do not overlap between sites, a distinction in the level of community closure where the threshold happens is observed. Values of Sup*F* test, the breakpoint and the confidence intervals (CI) presented in the table. *p ≤ 0.05; **p ≤ 0.01; ***p ≤ 0.001.

	LFL			HFL		
Attribute	sup(*F*)	Breakpoint	CI	sup(*F*)	Breakpoint	CI
Relative Height	75.45***	0.63	0.628 - 0.648	156.97***	0.54	0.532 - 0.549
Relative Stem Bark Thickness	79.2***	0.63	0.628 - 0.648	82.71***	0.52	0.505 - 0.532
Specific Leaf Area	98.73***	0.63	0.628 - 0.648	143.22***	0.52	0.512 - 0.525
Wood Density	16.13**	0.66	0.599 - 0.790	72.56***	0.52	0.514 - 0.548
Soil Organic Matter	26.92***	0.68	0.633 - 0.707	39.88***	0.52	0.501 - 0.549
Soil Nitrogen	24.58***	0.73	0.705 - 0.794	111.83***	0.52	0.501 - 0.525
Soil Phosphorus	55.01***	0.68	0.635 - 0.687	65.81***	0.52	0.477 - 0.525
Soil Aluminum	29.81***	0.54	0.488 - 0.617	19.04***	0.62	0.486 - 0.673
Soil Sum of Cations (K + Ca + Mg)	8.02	0.73	NA	148.64***	0.54	0.525 - 0.548
Soil Sand	3.24	0.54	NA	43.35***	0.51	0.500 - 0.548
Soil pH	30.39***	0.58	0.489 - 0.628	36.6***	0.62	0.505 - 0.630

Table 2: Comparison of fitted models for the functional traits that presented a significant breakpoint in the Community Closure Index (CCI) gradient at the Low (LFL) and High (HFL) Fire Landscape. R-squared values are presented for the linear (LM) and piecewise (PM) model. Whenever there were a significant breakpoint, and the piecewise model fitted better and presented a lower AICc value than the linear, we could affirm that there was a threshold relationship between CCI and the parameter being observed. An ANOVA test was used to help to compare the two models. *p ≤ 0.05; **p ≤ 0.01; ***p ≤ 0.001.

	LFL				HFL			
	R^2		ANOVA	ΔAICc	R^2		ANOVA	ΔAICc
Attribute	LM	PM	*F*2.46	(LM - PM)	LM	PM	*F*2,94	(LM - PM)
Relative Height	0.44	0.57	7.96**	10.02	0.54	0.6	8.19***	11.35
Relative Stem Bark Thickness	0.47	0.63	11.40***	15.29	0.33	0.48	14.81***	22.46
Specific Leaf Area	0.42	0.64	16.26***	21.9	0.49	0.61	15.63***	23.73
Wood Density	0.01	0.16	5.06*	5.1	0.38	0.43	5.47**	6.4
Soil Organic Matter	0.18	0.3	5.13**	5.23	0.14	0.22	6.05**	7.47
Soil Nitrogen	0.14	0.24	4.00*	3.18	0.34	0.45	11.20***	16.56
Soil Phosphorus	0.32	0.54	12.33***	16.62	0.29	0.38	7.50**	10.12
Soil Aluminum	0.19	0.42	10.78***	14.38	0.11	0.14	2.81	1.3
Soil Sum of Cations (K + Ca + Mg)	NA	NA	NA	NA	0.48	0.59	14.22***	21.43
Soil Sand	NA	NA	NA	NA	0.24	0.27	3.24*	2.14
Soil pH	0.15	0.37	9.29***	12.12	0.26	0.29	2.78	1.23

3.3 Soil Breakpoints

Some soil traits, just like the vegetation functional traits mentioned above, presented a threshold between more open and more closed communities. In general, communities with higher CCI presented higher levels of soil organic matter and nutrients. Breakpoints in the CCI gradient were significant at both sites for soil organic matter (OM), nitrogen (N), phosphorus (P; Fig. 4), aluminum (Al), pH and cation exchange capacity (CEC; Table 1). For the soil traits sum of cations (K + Ca + Mg) and sand content, the breakpoint was only significant at the HFL (Table 1). The piecewise model fitted better for all parameters which presented a significant breakpoint, except for Al and pH at the HFL, which was not significant when comparing both models with the ANOVA (Table 2), indicating the lack of a threshold relationship for these parameters.

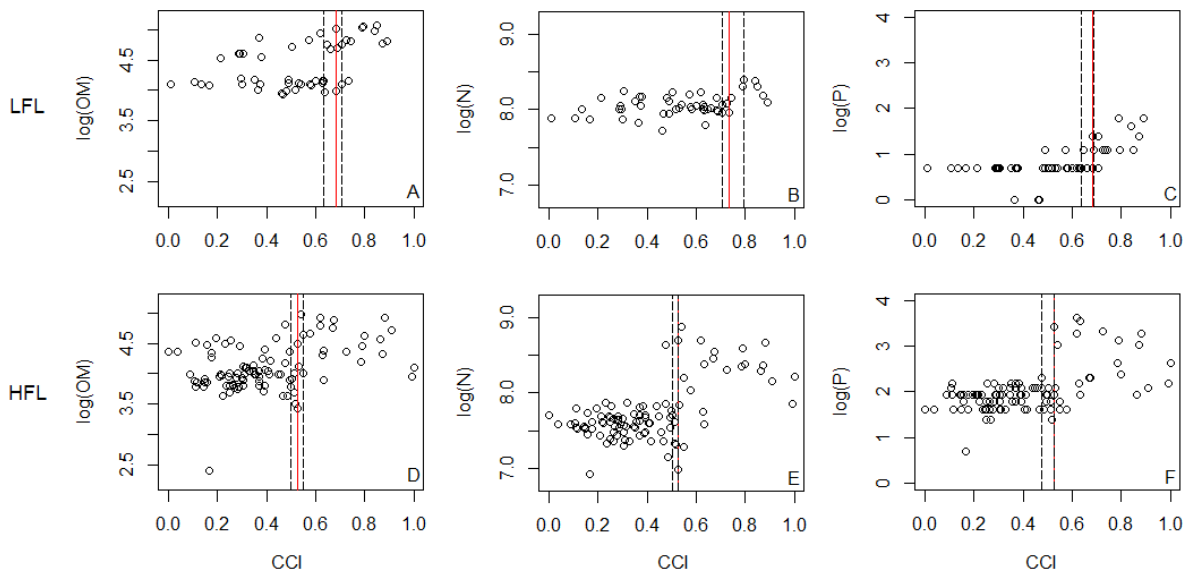

Figure 4: Soil parameters thresholds in a Community Closure Index (CCI) gradient at the Low (LFL) and High (HFL) Fire Landscape. The parameters presented are organic matter (OM), nitrogen and phosphorus soil content for the LFL (A, B and C, respectively) and the HFL (D, E and F, respectively). Aluminum and sand content, soil sum of cations and pH did not present a threshold relationship and were not included in the figure. Breakpoints are represented by solid red lines and the confidence intervals by dashed black lines. Similar to what occurred with the plants functional traits, the threshold occurs in more closed communities at the LFL when compared to the HFL. All breakpoints were significant (p < 0.05).

The confidence intervals for all soil traits, except soil Al and pH (not shown), did not overlap when comparing the thresholds between the LFL and the HFL (Table 1), indicating again that there is a distinction in the level of community closure at which the threshold happens at each site.

Taking into account only the vegetation attributes and soil traits that presented a significant breakpoint and a better fit with the piecewise model, we calculated a mean threshold for the CCI gradient at each site. For the LFL the mean threshold was located at CCI = 0.64 ± 0.055 and for the HFL at CCI = 0.52 ± 0.009. Through this separation of communities with two distinct vegetation states of contrasting attributes, we could compare the fire activity at each state (Fig. 5). We labeled plots with CCI higher or equal the mean breakpoint value as forest plots, and with lower CCI as savanna plots.

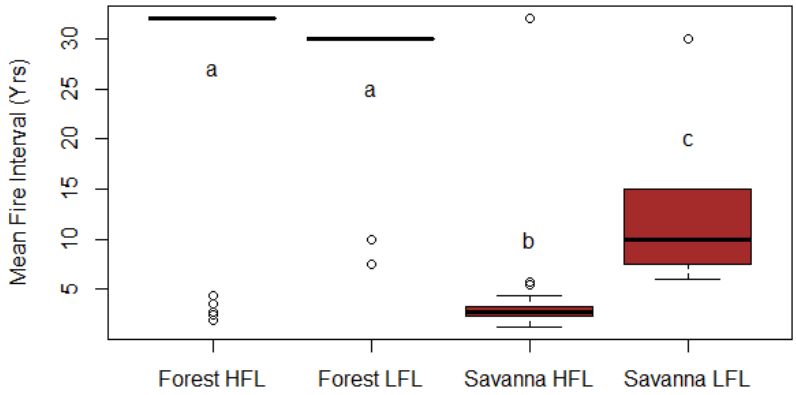

Figure 5: Fire activity of savannas and forests at the Low (LFL) and High (HFL) Fire Landscape. Savannas clearly burn more often than forests in both areas, and the more frequent fire activity at the HFL savanna plots is observable. This distinction between fire activity in the savannas of each site could be attributed to differences in soil resource availability (Fig. 6). In both forests, fire activity was similar. Different letters represent significant differences between variables (values of $p < 0.05$ considered significant).

3.4 Magnitude of Change

The vegetation traits that presented a threshold relationship, and therefore used for the magnitude of change analysis were relative height, relative stem bark thickness, SLA and wood density, while the soil traits were soil organic matter, N and P concentration, and soil cation exchange capacity. For all the traits analyzed, the magnitude of change was higher at the HFL when compared to the LFL (Table 3), and the Student's t-Test result ($t = -5.09$; $p < 0.001$) indicated that the differences between sites were significant.

Table 3: Magnitude of the breakpoints for traits and soil features showing significant threshold relationship at the Low (LFL) and High (HFL) Fire Landscape, respectively. The magnitudes differ between sites, and are larger at the HFL for all traits ($t = -5.09$; $p < 0.001$).

	Site	
Attribute	LFL	HFL
Relative Height	0.2570	0.5515
Relative Stem Bark Thickness	0.1801	0.6863
Specific Leaf Area	0.2040	0.4685
Wood Density	0.1587	0.1701
Soil Organic Matter	0.2142	0.4610
Soil Nitrogen	0.1172	0.5285
Soil Phosphorus	0.3009	0.5834

3.5 Soil Resources vs. Functional Traits

When comparing soil resources between vegetation states at the LFL and the HFL, we observed no differences in N concentration between forests at both landscapes (Fig. 6A). We also observed higher concentrations of P at the HFL forests and savannas, when compared to the LFL forests and savannas, respectively (Fig. 6B). Forests at the HFL presented higher levels of the sum of cations (K + Ca + Mg) when compared with the LFL forests, although LFL savannas presented higher levels than the HFL ones (Fig. 6C). Concerning sand content, forests at the HFL presented lower levels than LFL forests, and HFL savannas presented lower levels than the LFL ones as well (Fig. 6D). As soil N is less limiting than soil P in old tropical ecosystem soils (Walker & Syers 1976; Elser *et al.* 2007), N concentrations were not considered when establishing a general soil resource availability comparison between landscapes (Table 4). Higher sand concentration is treated here as a reducer of soil resource availability, as better explained later in the discussion section. In general, the HFL soils presented higher resource availability in both forests and savannas when compared to the LFL, and also more accentuated differences between forests and savannas, while soils of LFL savannas and forests did not differ overall (Table 4).

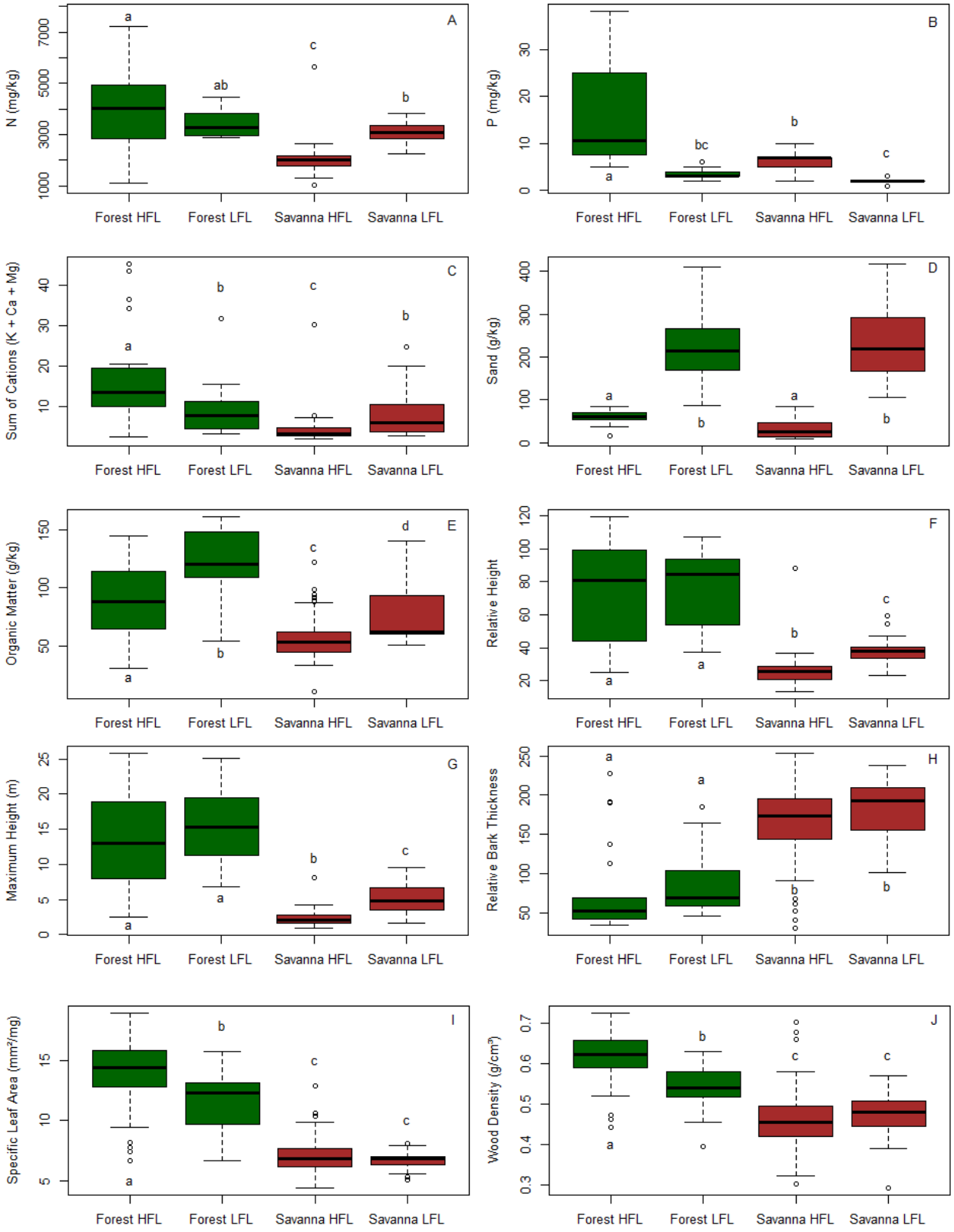

Figure 6: Soil resources and functional traits variation in forests and savannas at the Low (LFL) and High (HFL) Fire Landscape. Soil resource availability was higher at the HFL, in general. Communities height apparently did not respond to this resources distinction in forests, and responded inversely in savannas. Different letters represent significant differences between variables (values of $p < 0.05$ considered significant).

When comparing functional trait variation between forests of each site and savannas of each site, we observed no differences in the relative and maximum height of forest communities, and taller communities at LFL savannas when compared do HFL ones (Fig. 6F, 6G), which is the opposite of the expected for high soil resources. Though no statistical analysis was made to prove it, relative stem bark thickness apparently does not respond to soil resources differences (Fig. 6H). For the SLA and wood density traits, however, higher values were found at HFL forest communities, where soil resources are more available, when compared to LFL forests (Fig. 6I, 6J).

Table 4: General soil resource availability and fire activity at the Low (LFL) and High (HFL) Fire Landscape. The soil parameters considered for the resource availability comparison were phosphorus concentration, sum of cations and sand concentration. Forests and savannas at the HFL presented higher soil resource availability. Soil resources did not differ significantly between forests and savannas at the LFL. Forests at both sites burned with the same frequency, and savannas at the HFL burned more frequently than at the LFL.

		Site	
		HFL	LFL
Soil Resource Availability	Forest	>	<
	Savanna	>	<
	Forest vs. Savanna	≠	=
Fire Activity	Forest	=	=
	Savanna	>	<
	Forest vs. Savanna	≠	≠

Finally, to check which parameters better explained variations in community closure, we fitted a multiple regression using soil properties together with fire activity as explanatory variables. The model which best fitted for the HFL data included only mean fire interval (MFI) as explanatory variable (Eq. 1; $R^2 = 0.57$, $p < 0.001$), and the one which best fitted for the LFL data included MFI and soil P concentration (Eq. 2; $R^2 = 0.46$, $p < 0.001$).

Eq. (1) $CCI = 0.231 + 0.003\ MFI$

Eq. (2) $CCI = 0.19 + 0.008\ MFI + 0.076\ P$

4. DISCUSSION

The functional traits studied differed significantly between forests and savannas, as well as almost all of the soil parameters. Almost all traits analyzed, including plant and soil traits, presented a significant breakpoint at some part of the community closure gradient and a threshold relationship, indicating strong evidence of an abrupt functional separation between two distinct vegetation states. These findings agree with other studies (Hoffmann *et al.* 2005, 2012; Rossatto *et al.* 2009).

Fire activity is much more frequent in savannas than in forests. Thus, the vegetation structure is under constant disturbance, and plant traits are under the influence of a strong selective pressure exerted by fire in savannas (Bond *et al.* 2005; Staver *et al.* 2011a, 2011b). Savanna plots at both studied sites together presented a mean fire interval more than two times shorter when compared to forest plots, indicating frequent fire activity in savannas of our study sites as well.

Taller woody plants were more commonly found in more closed communities, or forests. The selective advantages of growing in height to reach light above the closed canopy could explain this pattern. However, in more open communities (savannas) the high cost in construction and maintenance of the stem along with the low advantages brought by growth in height at this system (light is not limiting) could be selecting plants with lower heights and higher investment in other traits (Falster & Westoby 2003; Hoffmann *et al.* 2003; Lawes *et al.* 2011). As an example, we found a significant higher relative stem bark thickness for the vegetation in savanna plots, suggesting a higher investment in this trait for savanna trees. Lawes *et al.* (2013) proposed that investing in a relatively thick bark lowers the costs of acquiring an absolute thick bark, and at the same time grants protection for smaller stems against fire, while investing in bark at an early life stage would be really costly for forest trees in a light limited environment (Hoffmann *et al.* 2003), reinforcing the suggestions made from our results. However, the selective pressure exerted by other system conditions, and their relation with other functions of the bark cannot be ignored. The water storage function of the inner bark, which increases alongside bark thickness (Rosell *et al.* 2014), suggests that drier and warmer environments can favor the occurrence of thicker barks (Rosell 2016).

In turn, SLA and wood density traits behaved the opposite way: both were significantly higher in forested plots. SLA is a trait related to the photosynthetic rate per leaf mass unit, and as proposed by Westoby (1998), it is a trait that reflects return in investment, that is, high SLA results in a quick payback for the plant (Poorter & Remkes 1990; Reich *et al.* 1992). This could possibly explain the selective advantages that high SLA levels bring to forest tree species, which need to establish and grow rapidly in the closed canopy shaded communities. Wood density apparently presented a less accentuated variation along the CCI gradient. However, the statistical analysis resulted in a significant breakpoint, and indicated the presence of a threshold relationship between this trait and the CCI. This trait is commonly related to tree structure, that is, higher wood density supports a higher and wider crown (King *et al.* 2006), which is a common characteristic of forest trees. Another benefit brought by increasing levels of wood density is related to cavitation resistance. It is critical for tall trees to avoid cavitation in order to grow in height (Koch *et al.* 2004), and as proposed by Hacke *et al.* (2001), wood density is related to resistance to cavitation (although this relationship is not consensual among authors). This could in part explain the pattern we found at the studied sites, with tall and dense wooded trees occurring in forests, while the opposite happens in savannas.

All these abrupt shifts in the functional trait values along the CCI gradient clearly indicate the co-occurrence of savannas and forests as alternative vegetation states under the same climate envelop. The distinct fire activity between vegetation states lead us to think of fire as the main factor driving the observed differences in traits. Undoubtedly, fire exerts a strong selective pressure in plant populations in savannas, and as shown by Simon *et al.* (2009) some Cerrado lineages started to diversify four million years ago or less, at the same time of the flammable C4 grasses increased dominance. However, we cannot assume that fire is the only responsible, as species current occurring in Brazilian savannas are a result of millions of evolutionary years, and their traits could be also related to many other selective pressures acting over their populations over the years (Rosell 2016).

Soils at the HFL, in general, presented higher resource availability in both forests and savannas, when compared to LFL forests and savannas, respectively. Comparing forests with savannas at the LFL resulted in similar levels of soil resources. Soil P concentration and sum of cations could be affecting primary

productivity and other plant growth processes (Porder *et al.* 2007; Vitousek *et al.* 2010; Wright *et al.* 2011). Sand concentration in our case can be used as an indicator of water availability in the soil, as the mean annual precipitation (MAP) of both sites is similar. Thus, lower sand levels indicate more soil water retention. Low water availability interfere directly on plant functions, including carbon dioxide assimilation by leaves and roots nutrient uptake, affecting plant growth and development (Schulze 1991). Regarding soil organic matter, forests at the LFL presented higher levels when compared to the HFL forests, and the same was observed in savannas. This pattern was the opposite from what was observed for resource availability in general, indicating that organic matter may be contributing to soil resources, but is not the main factor determining it.

Regarding our first question (1) how soil properties and fire activity affect the structure of savannas and forests at local scale?, no differences were found between community relative and maximum height of forests at the High and Low Fire Landscapes, indicating that soil is possible not affecting this community structure parameter. In savannas, however, tree height was higher for LFL communities, where soil resources were less available. These results indicate not only that soil properties are not influencing tree height in savannas, but that another factor is selecting for lower trees at the HFL. As fire activity is more frequent at HFL savannas, fire could be a possible answer, as frequent fires could be selecting woody trees with less investment in height growth and higher investment in fire-survival related traits (Williams *et al.* 1999; Hoffmann *et al.* 2003; Lawes *et al.* 2011).

Specific leaf area (SLA) and wood density presented higher values at HFL forests when compared to LFL forests. As HFL forests presented higher soil resources as well, this could indicate a positive relation between soil attributes and these two traits in forests (Westoby 1998; Ordoñez *et al.* 2009). All plant functional traits differed when comparing forest and savanna communities of the LFL and the HFL. Even soil resources not differing between LFL forest and savanna communities, plant functional traits differed, indicating that some other factor is selecting for the distinction of these two traits likewise. As fire activity substantially differed between the two vegetation states at both sites, fire again is a possible candidate to explain these variations.

Finally, the multiple regression indicated mean fire interval as a good predictor variable explaining variations in community closure at both sites, and soil P as an important variable at the LFL, as well. All these results pointing to fire as the main reason of community structure shaping do not exclude soil resources importance. C4 grasses respond positively to soil P (Hetrick *et al.* 1990), other soil nutrients (Medina 2013) and water availability (Caldwell *et al.* 1977; Baruch & Fernández 1993). As C4 grasses are the main fuel used by fire, successful establishment and growth, and higher productivity of these grasses would allow the formation of a continuous grass layer and higher availability of fuel for fires. Thus, soil resource availability is, through direct and indirect processes, also shaping communities in forests and savannas. Human action cannot be excluded when trying to explain fire activity distinction between sites, as well. As the sampling was held inside two protected areas, it is possible that distinct management practices interfered differently in the fire activity of each site.

The threshold relationship was found for all plant functional traits and almost all soil traits analyzed. As expected, we observed distinct threshold positions in the CCI gradient at each site, without overlaps in the confidence interval. The fire activity analysis also led us to distinguish fire regimes between the two landscapes, what could indicate fire as a responsible disturbance factor affecting the level of community closure where the threshold occurs. In response to our second question (2) how the location and magnitude of functional trait thresholds in savanna-forest gradients differ between sites with distinct fire regimes and soil resource availability?, our results suggest that the frequent fire activity at the HFL is further inhibiting the closure of savanna communities by top-killing woody trees not protected from fire and not permitting forest trees individuals to establish and grow (Hoffmann *et al.* 2003, 2012; Lawes *et al.* 2011). In the meanwhile, longer fire-free periods at the LFL are permitting savanna woody tress to occupy open spaces and eventually become more closed communities, and that would explain lower CCI levels for savanna plots at the HFL and higher at the LFL. Forest expansion over savannas is not observable through the threshold between functional traits and the community closure gradient. This occurs because communities that shift to forests will present simultaneously higher CCI and individuals with characteristic forest traits. At the HFL, the presence of functional traits characteristic of forest species in lower CCI levels than expected (if

compared to the LFL), indicates that frequent fire action is possibly opening the communities there, reducing the CCI of forest plots but still leaving many forest trees alive. If this process continue to happen, it is possible that the opening in the canopy will permit the increase of C4 grasses in the understory, which in turn will increase fire frequency even more, possibly leading to a transition from a forest to a savanna state in the forest fragments found at the HFL (Bond *et al.* 2005; Bond 2008; Hoffmann *et al.* 2012).

Regarding the magnitude of the change, we found strong evidence that both fire and soil resources are affecting it. The magnitude was larger for all HFL plant functional traits, indicating a more abrupt shift (spatial, not temporal) in the forest-savanna trait transition along de community closure gradient. Fire exerts a strong selective pressure in plant functional traits, favoring individuals that invest more in bark thickness instead of height and other traits (Hoffmann *et al.* 2003; Lawes *et al.* 2011, 2013). Forest tree individuals would be favored by traits that increase photosynthetic rate, allowing for a fast establishment and growth (like SLA), and traits that help to support greater heights (like wood density), in order to reach light in the canopy (Poorter & Remkes 1990; Reich *et al.* 1992; Westoby 1998; King *et al.* 2006). The higher frequency of fire activity at the HFL may be accentuating this pressure exerted by fire, which together with more contrasting soil resource availability between savannas and forests is possibly causing the larger functional trait magnitude of change. Meanwhile, at the LFL, lower fire activity and almost no differences in soil resources when comparing savannas to forests could be smoothing the differences in functional traits of the two vegetation states. The transition is still abrupt, as shown by the threshold relationship between the traits and de CCI, but at the LFL it is slightly smoother.

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6. APPENDICES

6.1 Appendix A

Table A1: Fitted logistic regression for functional traits and soil parameters that presented a significant breakpoint in the CCI gradient at the LFL and the HFL. McFadden's Pseudo R-squared and the differences of AICc values between the linear model (LM) and the piecewise model (PM) against the logistic model (LgtM) are presented. In most cases, AICc values were higher for the logistic model when compared to the linear and piecewise ones, indicating a worse fit.

	LFL			HFL		
	$R^2_{McFadden}$	ΔAICc		$R^2_{McFadden}$	ΔAICc	
Attribute		(LM - LgtM)	(PM - LgtM)		(LM - LgtM)	(PM - LgtM)
Relative Height	0.22	-32.43	-42.45	0.31	2.65	-8.7
Relative Stem Bark Thickness	0.3	-5.16	-20.44	0.25	49.41	26.95
Specific Leaf Area	0.28	-47.34	-69.24	0.23	-85.49	-109.23
Wood Density	-0.004	-110.45	-115.55	0.13	-207.91	-214.31
Soil Organic Matter	0.08	-29	-34.23	-0.01	-9.98	-17.45
Soil Nitrogen	0.05	-126.59	-129.78	0.18	-43.82	-58.26
Soil Phosphorus	0.18	-31.5	-48.12	0.1	-6.24	-16.36
Soil Aluminum	0.02	15.28	0.9	0.04	-70.47	-71.77
Soil Sum of Cations (K + Ca + Mg)	NA	NA	NA	0.37	84.8	63.37
Soil Sand	NA	NA	NA	0.13	48.14	46
Soil pH	0.09	-216.33	-221.84	0.16	-321.59	-322.82

7. ATTACHMENTS

7.1 Attachment A

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DECLARAÇÃO

Em observância ao **§5º do Artigo 1º da Informação CCPG-UNICAMP/001/15**, referente a Bioética e Biossegurança, declaro que o conteúdo de minha Dissertação de Mestrado, intitulada "***The Role of Fire and Soil Resources in Forest-Savanna Structure and Transition Dynamics***", desenvolvida no Programa de Pós-Graduação em Ecologia do Instituto de Biologia da Unicamp, não versa sobre pesquisa envolvendo seres humanos, animais ou temas afetos a Biossegurança.

Assinatura: _____
Nome do(a) aluno(a): Paulo Negri Bernardino

Assinatura: _____
Nome do(a) orientador(a): Rafael Silva Oliveira

Data: 25 de Agosto de 2016

7.2 Attachment B

Profa. Dra. Rachel Meneguello
Presidente
Comissão Central de Pós-Graduação
Declaração

As cópias de artigos de minha autoria ou de minha co-autoria, já publicados ou submetidos para publicação em revistas científicas ou anais de congressos sujeitos a arbitragem, que constam da minha Dissertação/Tese de Mestrado/Doutorado, intitulada **"The Role of Fire and Soil Resources in Forest-Savanna Structure and Transition Dynamics**, não infringem os dispositivos da Lei n.° 9.610/98, nem o direito autoral de qualquer editora.

Campinas, 25 de Agosto de 2016

Assinatura : _____
Nome do(a) autor(a): **Paulo Negri Bernardino**
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